

This shell differs only in shape, the outstanding point being the height of the spire, which is often twice as long in a specimen of *altispira* as in a similar sized specimen of the species. The shell is narrower, with the spire more conical and the aperture quite slender in comparison. A true *magnifica* is similar in appearance to a *Melo*, the aperture being extremely large and outer lip rounded, while the spire is short and very ventricose. In the case of *V. magnifica* the posterior canal ends quite close to the suture, while in *altispira* the canal ends two or three times further away from the suture.

Hab.: Usually occurs in deep water. They have been trapped alive as deep as 60 fathoms, and as a general rule the deeper they are the longer and more slender the shell.

Loc.: Port Stephens to Botany Bay.

#### COMPARISON OF MEASUREMENTS.

	<i>altispira</i>	<i>magnifica</i>
Total length .....	9 $\frac{3}{8}$ "	9"
Length of aperture .....	7 $\frac{1}{8}$ "	7 $\frac{7}{8}$ "
Length of spire .....	2 $\frac{1}{4}$ "	1 $\frac{1}{8}$ "
Width of aperture .....	3 $\frac{1}{8}$ "	3 $\frac{3}{8}$ "
Width of shell .....	5 $\frac{1}{4}$ "	5 $\frac{1}{8}$ "
Width of shoulder .....	4 $\frac{3}{8}$ "	4 $\frac{5}{8}$ "

*Livonia mamilla leucostoma*, subsp. nov.

(Plate xxvi., fig. 3)

Length: 200 — 250 mm.

Breadth: 130 mm.

Shell ovate, spire one-fifth of length, nucleus consists of one large mamilliform whorl with the apex very eccentric and lower down on one side; surface is wrinkled and of white to dirty white in colour. There are two and one-half post nuclear whorls; suture distinct and irregularly undulated. Lip thin and strongly recurved, extended slightly outwards and advancing upwards three-quarters of the height of the penultimate whorl. Anterior canal short, broad and open. Columella shallow, showing three distinct plaits, the upper one less pronounced.

Colour, tan, with a darker brown band below the suture; to a dirty white in some shells. Shell longitudinally irregularly marked with a broken design of brownish triangular streaks. Aperture is of a pure white porcelain colour. Base of last whorl is darker, showing distinctly a sinuation.

In shape and structure this shell agrees with the species, the colour of the aperture, which is brown in the species, and nucleus being the only distinction.

It is believed that this shell does not grow quite as large as the species and is generally thinner, the largest shell known to the author being 11 $\frac{1}{2}$  inches against 13 inches in the species.

Distribution: Generally below 80 fathoms around Gabo Is. in southern New South Wales seas.

Specimens have been reported as being very thin and almost pure white and coming from greater depths, but none have yet been brought to land.

#### Family FUSINIDAE.

*Propefusus compositis*, sp. nov.

(Plate xxvi., fig. 4)

Length: 70 — 100 mm.

Shell fusiform; spire long, pointed, almost half length of shell, rounded with rather a deep suture and consisting of seven whorls; nucleus white and containing

two whorls which end in a sharp point; aperture ovate; canal long, narrow slightly curved and open.

The penultimate whorl has six prominent encircling ridges with a smaller one suturally and an evanescent one anteriorly; the interstices rather wide and longitudinally ridged with about 15 elevated ribs which may become less marked and up to twenty on the last whorl. In some the longitudinal ridges are even more prominent and fewer in number. Inside the aperture the encircling ridges leave corresponding hollows through the rather thin outer wall, giving it a corrugated appearance.

The shell is coloured dirty white and covered with a tough thin brown epidermis. The longitudinal ridges are marked with a rusty line which shows clearly through the epidermis and giving it a brindled appearance.

Hab.: These shells would be more inclined to live in a rocky rather than a sandy environment, as they are only very occasionally caught. They are believed to live in 50-80 fathoms.

Loc.: Gabo Is. of southern New South Wales and extending into Victorian waters.

EXPLANATION OF PLATE xxvi.

Fig. 1: *Cymbiolena magnifica altispira* Mayblom.

Fig. 2: *Cymbiolena magnifica magnifica* Shaw & Nodder.

Fig. 3: *Livonia mamilla leucostoma* Mayblom.

Fig. 4: *Propefusus compositis* Mayblom.

Photo.—G. McGrath.



## BIOLOGY OF THE REED-BEES.

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WITH DESCRIPTIONS OF THREE NEW SPECIES AND TWO ALLOTYPES OF  
EXONEURA.

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By TARLTON RAYMENT, F.R.Z.S.

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(Plate xxvii.-xxxii., text-figures 1-2)

### INTRODUCTION.

The author is now able to draw a detailed picture of the biology of these remarkable bees, but this would not have been possible without the co-operation of several enthusiastic collectors in the field, each of whom has contributed hundreds of specimens and many "nests", together with a number of helpful observations. The author desires to place on record his appreciation of their conscientious endeavours.

The late J. E. Dixon, an old and respected fellow-member of the Field Naturalists' Club of Victoria, was the first to bring a twig of dry *Melaleuca ericifolia* from Frankston, Victoria. He said it had contained a nest of *Exoneura*, but did not know which species had bored the stem; only the empty gallery remained; circa 1930.

In 1935, John Hardcastle, Junior, White Swamp, on the border of New South Wales and Queensland, forwarded a nest of *E. perpensa* Ckll., but only adults were present in the twig, which had been cut from "brush box", *Tristania conferta*. In the same year, R. Willey, Woy Woy, New South Wales, collected a plant-stem occupied by imagines of *E. hamulata* Ckll. No larvae were present in either of these "nests".

Alex. Holmes, editor of the magazine "Bird World", Woollahra, New South Wales, sent a twig of *Banksia* containing eggs, larvae, and imagines of the species that bears his name. That was in 1940; the first record of the larvae.

In 1944, Norman Rodd, Lane Cove, Sydney, New South Wales, went into the field and was very successful in collecting twigs containing galleries, eggs, larvae and adults of several species of *Exoneura*, especially *E. roddiana* Raym.

In the same year, Owen Dawson, on service with a radar unit, R.A.A.F., began to search for reeds and sticks drilled by these bees, and he, too, found the "nests" of several species, each of which contained eggs, larvae and adults. Newton Lawson, Canberra, Federal Territory, also sent a "nest" about that date.

The author himself had collected the nesting galleries of several species during his excursions into the other States of the Commonwealth, and Rica Erickson, Bolgart, Western Australia, also found many twigs about 90 miles north of Perth.

In October, 1948, C. E. Chadwick, entomologist, Department of Agriculture, Sydney, New South Wales, discovered a series of "nests" in galls, all of which were taken at Bradfield Park, near Sydney, and these proved to be occupied by *E. concinnula* Ckll.

It will be seen, therefore, that the research has extended over many years, and it is now known that the *Exoneuræ* are very remarkable bees, not only because of the unique appendages—like "arms" and "hands"—of the larvae, but also for the communal cell, which also is unique, and the progressive feeding of the larvae with a glandular secretion by the adults over a long period. The sharing of the work among several sisters undoubtedly elevates the genus to a social status, although the members of the family are few in number. *Exoneura*,



then, occupies a position between the populous social bees *Melipona* and the solitary wild bee *Lestis*, which remain at the original nest until the progeny emerge. The former bee builds wax cells, the latter nests in plant-stems.

Kerr (1946) demonstrated that in *Melipona*, an American genus of comb-building social bees closely allied to the Australian *Trigona*, the castes are due to genetic factors, and not to differences in food. There are no specialised cells, not even for the queen. In *Exoneura* there are no castes and no cells, only the two sexes.

The author's researches in the Hymenoptera are assisted by a Grant from the Trustees of the Commonwealth Science and Industry Endowment Fund.

#### SYSTEMATIC POSITION.

Order HYMENOPTERA.

Suborder HETEROPHAGA.

DIVISION XYLOCOPIFORMES.

Superfamily APOIDEA.

Family CERATINIDAE.

Genus *Exoneura* Smith.

*Exoneura* Smith, Cat. Hym. B.M. ii., p. 232, 1854. Genotype, *E. bicolor*. *Id.* Cockerell, Ann. Mag. Nat. Hist. (7), xvi., p. 465, 1905; Aust. Zool. vol. vi., pt. ii., pp. 148 and 153, 1930; *Id.* Rayment, A Cluster of Bees, p. 476, 1935.

#### MORPHOLOGY.

Small, soft-bodied bees, with a smooth shining integument; a long slender glossa; often with ivory-coloured marks on the clypeus; anterior wings with only one recurrent nervure. The majority of the species have a black head and thorax and a red abdomen, but there is a group entirely black. The bees have little pubescence, but the males are, anomalously, often more hairy than the females.

Cockerell (1930) regarded *Exoneura* as an Australian derivative from the African *Allodape*. "It is an example of an Australian genus which is less primitive than its relatives in the other parts of the world." The present research demonstrates that the larval appendages have a parallel in the African genus; there is a long-continued progressive feeding of the larvae, and the bees are truly social in habit.

The smallest of the described species is *E. parvula* Raym., which is only 3.5 mm. in length, with a black head and thorax and a red abdomen. It was described from Marysville, Victoria (F. E. Wilson), but it has since been taken near Sydney, New South Wales (Alex. Holmes).

Another small bee, *E. ploratula* Ckll., is 4.5 mm. in length, and entirely black, having no pale markings on the "face". W. W. Froggatt, the well-known entomologist, Sydney, collected it on flowers of *Angophora*. *E. botanica* Ckll. is another small, all black species, only 4.5 mm. in length. *E. gracilis* Ckll. described from Queensland (H. Hacker) is very small.

The largest *Exoneura* described is *E. grandis* Raym., and this belongs to the group with a black head and thorax and a clear ferruginous-red abdomen. It measures 10 mm. in length, a fine robust species without any pale markings on the "face". The type was collected by the author on flowers of the bramble, at Caulfield, Victoria.

Clarence Borch and Erasmus E. Wilson, both of the Field Naturalists' Club of Victoria, obtained several "new" males by sweeping with a net over bracken ferns in the Grampians Range, Victoria, and *E. xanthoclypeata* Raym. and *E. bicincta* Raym. were also obtained in this way.

Although the genotype, *E. bicolor* Smith, was described from Perth, the author has few *Exoneurae* from Western Australian, only four species, whereas the

related genus, *Allodapula* Ckll. is much better represented in the areas of low rainfall. *Neoceratina* Perk. is comparatively rare, and so far has been taken only in New South Wales.

#### SPECIFIC DESCRIPTION.

##### *Exoneura angulata*, sp. nov.

Type: Female. Length: 7 mm. approx. Black, with red abdomen.

Head black, with the parts angulated from eyes down to antennae; from antennae up to carina of frons; clypeus lying as a low plane, so that the whole face is excavated, but on different planes, and is very distinctive; clypeus suffused with reddish, some minute punctures; supraclypeal area forming the base of the excavation; vertex with large angulated areas above the compound eyes which converge slightly below; node-like swellings surround the ocelli; a few smoky hairs; genae with a microscopic lineation; even the genae are angulated apically; labrum suffused with red; mandibulae reddish, darker apically and basally; antennae black, obscurely brown beneath on apical half.

Prothorax with a few white hairs; tubercles black, with an ochreous fringe; mesothorax black, polished, with an excessively delicate tessellation, a few large punctures, and very scattered smoky hairs; scutellum similar; postscutellum rougher; metathorax black, with a comparatively coarse scale-like sculpture; the pleura have the most hair, which is ochreous on the polished plates; abdominal dorsal segments clear chestnut-red without any black markings, apical hair black and bristly; ventral segments red.

Legs black, femora apically, tibiae and tarsi all of a darker red, with much black hair on the hind tibia, otherwise the hair is golden, especially the tufts on anterior coxae; tarsi red, with golden hair; claws red; hind calcar red, much curved; tegulae reddish, with blackish suffusion; wings slightly yellowish, long, very iridescent; nervures sepia; second cubital cell greatly contracted at apex; pterostigma dark-brown; hamuli five, weak, unevenly spaced.

Locality: Dandenong, Victoria, 2nd November, 1948. Owen Dawson.

Type in the collection of the author.

Allies: *E. excavata* Ckll., which is larger and darker red; *E. subexcavata*, sp. nov., which has a bright yellow T on the clypeus.

By the structure of the larvae the new species is close to *E. richardsoni*, sp. nov., which was nesting in close proximity in the garden of W. R. Richardson, Esq., at Essex Park. The larva of *albolineata* Ckll. has two large "arms" laterally, each with two "fingers", *E. angulata* has only one "arm" laterally.

##### *Exoneura subexcavata*, sp. nov.

Female: Length, 7 mm. approx. Black, with red abdomen.

Head transverse, polished black; face-marks creamy-yellow; frons deeply excavated around antennae; clypeus with a yellow, thick "T", on some specimens the stem is as wide as the bar; supraclypeal area rising to a fine carina that reaches the median ocellus; vertex with a few griseous hairs; compound eyes converge slightly below; genae similar to mesothorax; labrum reddish; mandibulae reddish; antennae black, obscurely lighter beneath.

Prothorax not visible from above, black; tubercles yellow, with fringe of white hair; mesothorax shining, black, a delicate sculpture, scattered punctures, sparse hair; scutellum and postscutellum similar; metathorax black, sculpture more defined; abdominal dorsal segments red, dusky at apex, with a few dark hairs; ventral segments somewhat darker.

Legs red, coxae, trochanters and extreme base of femora black, hair yellowish, except exterior of tibiae, where it is blackish; tarsi with golden hair; claws reddish;

hind calcar amber; tegulae amber; wings yellowish; nervures sepia; cells normal for genus; pterostigma amber; hamuli five, very weak.

Locality: Emerald, Dandenong Ranges, Victoria (8th December, 1934, Owen Dawson and Rayment).

Type in the collection of the author.

Allies: *E. abstrusa* Ckll., the contour of the face of which is different, since it lacks such large excavations. *E. excavata* Ckll., which has no yellow face-marks, but closest to *E. [a] simillima* Raym.<sup>1</sup>

On flowers of *Leptospermum* species.

*Exoneura albolineata* Cockerell.

(Records of the Australian Museum, vol. xvii., No. 5, Sept., p. 241, 1929.)

A long series of "nests" built in dry stems of garden Dahlia and Hydrangea, Bramble and Rose, at Dandenong, contained many nursing females, and it was observed that the pale markings of the face varied in the females of the same nest.

The lateral marks may be broad and long, narrow and short, and on some specimens reduced to mere dots, while the "T" of the clypeus may be bright yellow and clear, but in some the mark is subobsolete, and one bee had an entirely black face. Determination is complicated by the fact that two species will occasionally shelter amicably in one twig during inclement weather, and there is some evidence that they work together in the rearing of the brood. The type female has black legs, and these southern females have red legs, and they lack the black basal patch and bands on the abdomen, although the male has the basal black mark. The Victorian bees may be known as *E. richardsoni*, sp. nov.

*Exoneura richardsoni*, sp. nov.

Type, Male: Length, 5 mm. approx. Black, with red abdomen.

Head polished, transverse; lateral face-marks large, ivory-coloured, shaped like a eucalypt leaf, filling the space between the clypeus and the orbital margin; frons excavated about the scapes, but rising to a median ridge, with its base on the black supraclypeal area, the ridge becomes bifurcate at the median ocellus; vertex with a few smoky hairs; ocelli large; compound eyes bulging, converging below; genae large for the genus, microscopically lineate; labrum ivory, a few white hairs; mandibulae ivory; antennae black, scapes ivory in front.

Prothorax black, prominent, with numerous white hairs; tubercles black, with a fringe of dense white hair; mesothorax smooth, shining, with an excessively delicate tessellation; scutellum and postscutellum similar; mesothorax with a coarser tessellation, and considerable white hair laterally; pleura shining, with much long loose plumose hair; abdominal dorsal segments clear ferruginous red, a black patch on the basal one, a few dark bristles apically where the red is somewhat darker; ventral segments similar.

Legs of the same clear bright red, with black coxae, and trochanters partly black, hind tibiae and basitarsi excessively stout, with black bristles on the outer surface, the femora with much long white hair; tarsi red, with some pale hair; claws red; hind calcar, tegulae and axillae amber; wings yellowish, iridescent; nervures dilute sepia, the first recurrent received by the second cubital cell at its anterior fifth; second cubital cell contracted above to half the width of the base; pterostigma large, dark-brown; hamuli five, weakly developed.

Localities: Narre Warren, Victoria, September, 1950, Owen Dawson. Dandenong, Victoria, 5th November, 1948, Owen Dawson and Rayment.

1. The initial "A" was omitted from the specific name in the original description. See "Victorian Naturalist", Vol. 65, pp. 208-212, Jan., 1949.



Type and allotype in the collection of the author.

Allies: This male is easily separated by its remarkably stout hind legs, especially the broad basitarsi which, strangely enough, have an oval suturiform mark apically, and similar to that of the anterior leg of the primitive wasps *Guiglia queenslandensis* (Turner) in the Family Oryssidae.

The sexes were not taken *in cop.*, but the male was sheltering with a number of females, and it agrees structurally with them. Like certain other species of *Exoneura* the male has more hair than the female.

The type of *E. albolineata* Ckll. was described from Dorrigo, New South Wales, but that has long lateral marks on the face.

Larva: There are eleven appendages along each side of the larva, and there is a second row of very minute nodes on the ventral surface, so that each segment bears four nodes; the first is the smallest node; the second is the largest "arm" with three "fingers" and a stout "thumb"; third with two small "fingers"; fourth, fifth, sixth, seventh and eighth have small nodes, but the ninth, tenth and eleventh have long slender "fingers".

The larva of *E. albolineata* Ckll. has only three "fingers" on the largest appendage, and the second lacks the basal "finger" of the new species; the fourth, fifth, sixth, seventh and eighth have long "fingers", not small nodes. These differences warrant full specific rank.

Description of Male, *E. rufitarsis* Raym.

(Aust. Zool., vol. xi., part 3, p. 253, 1948.)

Allotype, Male: Length, 5 mm. approx. Black.

Head almost circular from the front; shining bright; face-marks deep ivory-yellow; frons with a fine high carina that reaches the basin surrounding the median ocellus; clypeus ivory-yellow, the apex widely truncated, but laterally the yellow is indented at the tentorial pits, but expanded basally; a few white hairs; supraclypeal area black; vertex with a few long pale hairs; compound eyes bulging, converging below; genae finely lineolate, a few pale hairs; labrum yellow, with scattered black dots; mandibulae black, simple, an obscure median amber patch (the female has three small teeth); antennae black, scapes obscurely yellow on a front line, a few long white hairs.

Prothorax with a few pale hairs; tubercles ivory-yellow, with a dense fringe of white hair; mesothorax shining bright, finely lineolate, a few short white hairs about the margin; scutellum similar; postscutellum rougher; metathoracic area large, coarsely tessellate, a few white hairs laterally; abdominal dorsal segments transversely finely lineate, a few coarse pale bristles; ventral segments similar.

Legs black, anterior and median tibiae largely red; the hind tibiae blackish; tarsi all red, the hind ones darkest, a few pale hairs; basitarsi with fine black dots; claws reddish-amber, a large empodium; hind calcar amber; tegulae shining black; wings hyaline, rather broader than usual, iridescent; nervures blackish-brown, strong, first recurrent entering the second cubital at its basal sixth; cells: second cubital contracted apically to half its width; pterostigma large, blackish-brown; hamuli four, very weakly developed.

Localities: Clyde, Gippsland, Victoria, 13th July, 1948, Owen Dawson; Danenong, Victoria, 3rd November, Owen Dawson and Rayment.

Allies: Dissection of two males shows that it is very close to *E. roddiana* Raym., which is smaller; the female having red scapes, and the male black, the reverse of what persists in *E. rufitarsis*. The clypeal stripe is conspicuous on the female of *E. roddiana*, but practically obsolete in the new species. The larvae of both have only one "finger" on the "arm". *E. roddiana* was described from Lane Cove, New South Wales. (See plate xxx., figs. 5 and 25.)

## METHODS AND MATERIALS.

The author used the following methods quite successfully. A dry twiggy branch of tea-tree, seven feet tall, was set up in a sheltered, warm, unfrequented part of the garden, and firmly secured to a couple of stout stakes. Dry stems of rose, hydrangea and bamboo were cut into lengths of about 25 centimetres. These had a diameter of 8 millimetres, and were tied vertically on the branch.

Larger stems were utilised, and a coarse knitting-needle thrust down into the pith, and into these cavities the original tubes containing the *Exoneura* "nests" were gently inserted without disturbing either the bees or the larvae. The original tubes should first be split carefully, and the two pieces put neatly together again before placing in the protective stem.

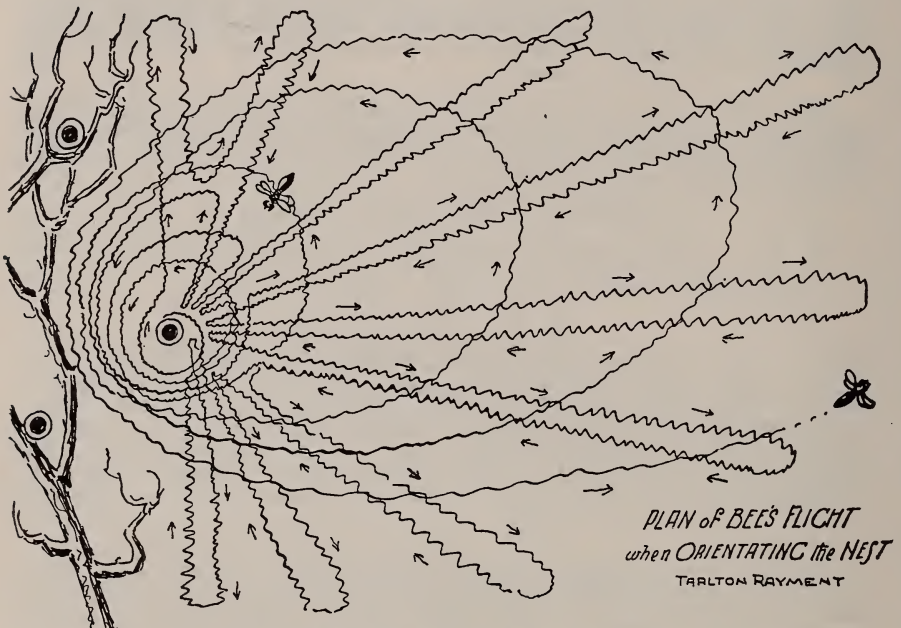


Fig. 1: Plan of the orientating flight of *Exoneura rufitarsis* Raym. The projecting dry twigs of the shrub preclude a circular course.

It is advisable to wind a few strands of wool, soaked in carbolic acid and oil, round the base of the branch to repel ants, for these pests will sometimes raid the nests of the *Exoneurae*, and carry off eggs and larvae should the nest be temporarily unguarded.

For continuous observation under a lens, thin tubes of plastic, blackened longitudinally, were used as "sleeves", which could be rotated to expose a slit in the nesting twig, or reversed again to exclude light. The end was closed with a plug of porous pith, through which a fine needle hole provided a trifle of ventilation; very little air is needed.

Using these simple arrangements, the author kept families under continuous observation for several weeks without detriment to either the adults or the larvae. Of course, a pollen-pudding must be provided for the adults, and the amount of honey used must not reduce it to a sticky mass, for then the females walk over it



and become incapacitated when the spiracles are clogged with the honey. The author experimented with his synthetic pollen and achieved some success, and he also supplied fresh pollen from the combs of the honeybee, and the larvae ate both kinds. A piece of pollen as large as a pea will be ample provision for a fortnight for a small family.

#### LOCALITIES

The "nests" of *E. rufitarsis* Raym. were obtained from Clyde, Gippsland and Dandenong, Victoria. The former district is thirty or so miles south-east of Melbourne, and six miles north of Tooradin, at the head of Western Port Bay. Geologically, the district is just within the old Red Sands of Sandringham, and which run on a finger-like extension through Cranbourne,  $2\frac{1}{2}$  miles west of Clyde. The extensive swamp-lands at Koo-Wee-Rup are only a few miles to the east, the contours, then, are flattened out.

The two or three hills of golden-yellow sand are probably old dunes, and there is a quarry which had been worked for the dark-red marl. Strangely enough, this material is known locally as "gravel", and its colour is, of course, due to the presence of iron. The red marl was used in many districts in the Red Sands area to dress roads and pathways. A very numerous colony of *Nomia australica* was studied in the marl, and its biology is awaiting publication.

The actual site of the colonies of *Exoneura rufitarsis* is on the margin of a swampy flat carrying a dense growth of low "manuka" tea-tree, *Leptospermum scoparium* and woolly tea-tree, *L. lanigerum*, say, four or five feet tall. On the higher levels is a number of needle-bushes of several species, such as *Hakea ulicina*, *H. nodosa* and *H. sericea*; the prevailing eucalypt is *E. viminalis*.

Seven "nesting" sticks were cut from a strong plant of golden spray, *Viminaria denudata*, which has a broom-like appearance, having more sticks than leaves, and, in summer, bearing masses of golden-yellow pea-shaped blooms; it is, of course, in the Family *Leguminosae*. Twenty-eight "nests" were taken at Dandenong during 1948.

Green twigs have no attraction for any bees, for the moisture in the sap favours the growth of moulds; consequently, only dry stems are utilised for "nesting". The sticks were about the base of the plant, at a height of from one to about three feet from the ground.

The 13th of July, 1948, was very cold, and the collector could not discover any flowers within a radius of half a mile of the "nests", but beyond that distance he found a wattle, *Acacia armata*, and a hedge of tree-lucerne, *Cytissus proliferus-albus*, in bloom. However, the *Exoneuræ* must have done better than the collector, for the triangular pollen-grains of some myrtaceous plant; thorny spherical ones from a composite, and plain spheres from some unknown source, were present in the ventriculus of the larvae, and they are quite different from the grains of the other two plants. How far the bees had to fly to reach their harvest could not be ascertained.

#### FLOWERS USED BY EXONEURÆ.

The bees have been taken in the field on many botanical species, and, like the hive-bee, thrive on a diet of mixed pollens. Whether or not they are constant to one plant on each harvesting journey has not been determined, but microscopical examination of the scopæ on homing bees seldom reveals an admixture of pollen-grains. What little contamination is present may be accidental.

The females have a scanty pubescence; the most conspicuous are the branched hairs forming the scopæ of the posterior legs; there is most hair on the femora and tarsi, and a few hairs on the gaster, but the bulk of the pollen is enmeshed in the scopæ. However, there are never at any time any large loads visible on the legs.

In all the many "nests" investigated by the author, he has never found any store of either honey or pollen, other than small individual puddings. The author has recorded that whereas the *Anthophorae* frequent a large number of botanical species introduced from overseas, the *Exoneuræ* definitely prefer the native plants, and this would seem to indicate the arrival of *Anthophora* in Australia at a comparatively recent date.

The following list of plants was compiled by the author and his collectors, and it has been checked by Messrs. P. F. Morris and J. M. Willis, National Herbarium. The author is indebted to these botanists for their co-operation:—

Family	Species	Locality	State
PITTSPOREACEAE	<i>Bursaria spinosa</i>	Hall's Gap	Victoria
"	" "	Mordialloc	Victoria
"	" "	Launceston	Tasmania
CARYOPHYLLACEAE	<i>Stellaria media</i>	Lane Cove	N.S.W.
LORANTHACEAE	<i>Loranthus</i> sp.	Gosford	N.S.W.
CRUCIFERAE	<i>Alyssum</i> sp.	Lane Cove	N.S.W.
GOODENIACEAE	<i>Goodenia ovata</i>	Grampians	Victoria
RUTACEAE	<i>Boronia pilosa</i>	Grampians	Victoria
ROSACEAE	<i>Rubus fruticosus</i>	Neerim	Victoria
"	" "	Oakleigh	Victoria
"	" "	Emerald	Victoria
"	<i>Rubus</i> (Loganberry)	Neerim	Victoria
LEGUMINOSAE	<i>Acacia pycnantha</i>	Grampians	Victoria
"	<i>Genista</i> sp. (Broom)	Macedon	Victoria
"	<i>Dillwynia ericifolia</i>	Black Sands	Victoria
"	<i>Platylobium formosum</i>	Emerald	Victoria
"	" <i>obtusangulum</i>	Grampians	Victoria
"	<i>Gunnii</i>	Emerald	Victoria
"	<i>Daviesia</i> sp.	Grampians	Victoria
MYRTACEAE	<i>Callistemon</i> sp.	Frankston	Victoria
"	<i>Angophora cordifolia</i>	Como	N.S.W.
"	<i>Eucalyptus</i> sp.	Como	N.S.W.
"	" "	Bundeena	N.S.W.
"	" "	Neerim	Victoria
"	" <i>corymbosa</i>		Victoria
"	<i>Kunzea ambigua</i>	Como	N.S.W.
"	<i>Calytrix sullivanii</i>	Grampians	Victoria
"	<i>Leptospermum arachnoideum</i>	Mt. Colah	N.S.W.
"	" <i>flavescens</i>	Como	N.S.W.
"	" "	Heathcote	N.S.W.
"	" <i>walkeri</i>	Toorak	Victoria
"	" <i>walkeri</i>	Dandenong	Victoria
"	" <i>scoparium</i>	Emerald	Victoria
"	" <i>mysinoides</i>	Grampians	Victoria
"	" "	Emerald	Victoria
"	<i>Melaleuca ericifolia</i>	Frankston	Victoria
"	" "	Cranbourne	Victoria
"	" <i>decussata</i>	Grampians	Victoria
"	" <i>squarrosa</i>	Grampians	Victoria
"	<i>Tristania conferta</i>	White Swamp	N.S.W.
LOGANIACEAE	<i>Logania floribunda</i>	Lane Cove	N.S.W.
UMBELLIFERAE	<i>Trachymene</i> sp.	Lane Cove	N.S.W.
VERBENACEAE	<i>Avicennia officinalis</i>	Cook's River	N.S.W.
LABIATAE	<i>Prostanthera lasianthos</i>	Emerald	Victoria
EPACRIDACEAE	<i>Leucopogon</i> spp.	Sandringham	Victoria
PROTEACEAE	<i>Banksia</i> sp.		N.S.W.
"	<i>Grevillea buxifolia</i>		N.S.W.
"	" <i>sericea</i>		N.S.W.
"	<i>Lomatia</i> sp.	White Swamp	N.S.W.
STYLIDIACEAE	<i>Stylidium graminifolium</i>	Mt. Buffalo	Victoria

Fig. 1

RUBIACEAE	<i>Plectronia attenuata</i>	Edungalba	Queensland
COMPOSITAE	<i>Aster subulatus</i> (Intro.)	Lane Cove	N.S.W.
"	<i>Hypochaeris radicata</i>	Inverloch	Victoria
"	<i>Olearia ramulosa</i>	Grampians	Victoria
"	"	Emerald	Victoria
"	<i>Taraxacum officinale</i> (Intro.)	Toorak	Victoria
"	"	Sandringham	Victoria
"	<i>Shasta</i> " Daisy "	Dandenong	Victoria

## ARCHITECTURE.

The majority of the "nests" investigated by the author have been in twigs, reeds, ferns or other plant-stems containing a soft pithy core. In every case the pith had been exposed, and in not a single instance was the fibrous woody wall attacked to effect an entry. The sticks are always vertical and quite dry, and the entrance invariably at the top. *Exoneura concinnula* occupied galls.

There is commonly an "iris" of wood-pulp constructed to reduce the diameter of a tube that is too large, and this ring near the "door", say, 2 mm. in thickness, is the only evidence of worth-while constructive craft; the rest of the work is a mere crude excavation of soft pith. At the base of the shaft there is sometimes a plug of thin parings, but the work is exceedingly elemental. No attempt is made to build any cell-divisions, for the interior of the plain tube is utterly devoid of cells, and consists of a true communal cradle shared by all, eggs, larvae, pupae, adult males and females. There is not a trace of any containers for food. When a couple of nests were built in a dry fern-frond, the galleries meticulously followed the soft pithy core, and where a harder line of woody fibre was encountered, the bees either went round it, or else ceased work at the obstacle. In places only the thinnest woody wall separated the two galleries, yet it was never once pierced by the bees.

It will be observed from the list of plant-stems utilised that only the softest of pith is excavated, and hard kinds are utterly neglected. One concludes that the bees are incapable of manipulating any stubborn material, for the small mandibles are not strongly formed, and their musculature is weak.

The twigs favoured by *E. rufitarsis* Raym. were of "Golden Broom", *Viminaria denudata*, and since seven "nests" were found on one plant, it would seem that the families prefer to labour in close proximity to each other.

That the *Exoneuræ* do not invariably seek pithy twigs, in which to establish their communal chambers, was demonstrated by Mr. C. E. Chadwick, entomologist, Department of Agriculture, Sydney, who forwarded a series of galls which had been formed on the stems of *Pultenaea stipularis* Sm. by the Buprestid beetle *Ethon* (probably the species *affine* Laporte and Gory); collected at North Shore.

These woody enlargements of the vegetable tissue were approximately 25 mm. in length, by 18 or so mm. broad, of irregular shape, but roughly subspherical, and each contained a cavity, more or less resembling a short wide tunnel. The wall was dark and hard, much too hard for the weak jaws of an *Exoneura*. The cavities were undoubtedly the work of the original tenant.

It was evident from this gall series that the bees in possession had made no attempt whatever to excavate the woody material, but had in every case used an entrance through a small hole which led to the interior—probably the exit hole. The interior walls were granular rather than smooth, and there was little, if any, draping with silky secretion to make them more acceptable, and no pithy structure could be found in even the normal twigs of the plant.

The collector observed that the interior of abandoned galls is usually cluttered with much frass left by the original tenant, but the *Exoneuræ* are thorough in their house-cleaning, and every fragment is meticulously taken out before they "settle in". The rubbish is removed with the mandibles.



The cylindrical eggs of the bees were attached to the wall by the usual agglutinative at the caudal pole, and the oldest larvae possessed appendages very similar indeed to those of the black species, *E. rufitarsis* Raym., that is, only one "arm", with a single "finger", is present on each side. There are not any abdominal nodes.

This is the first record of the nest and the larvae of *E. concinnula* Ckll., and it is even more evident that the species in this genus can be separated satisfactorily only after a study of the larvae and their appendages. This series of nests contained several eggs and fully developed larvae in October, and the biological cycle appears to conform to the typical pattern, a brood nursed by several sisters, in a communal cradle. The young larvae are fed over a lengthy period with a secretion of the pharyngeal glands, and later each larva receives its own individual pollen-ball. The excreta are ejected in three or four small single pellets, each less than 1 mm. in length, at 20-hour intervals.

These bees belong to the group with a red abdomen and an entirely black face, and are typical *Exoneura concinnula* Ckll. It was observed that several of the oldest larvae were lying criss-cross at one end of the chamber, without order, but this may have been due to shaking during transit in the mails.

However, this record is interesting, because it shows the adaptive character of the bees, and although the collector thought that the high sugar content of the galls may have attracted the bees, the author considers that this has no bearing on the bees' choice—the galls were merely suitable cavities, but if it be demonstrated in the future that these bees prefer the galls, then it is possible that some selective factor is involved.

In any case, the cavities in the galls are very small, and would be quite inadequate for a numerous brood. It is significant that only one or two females were present in each gall, and the largest number of larvae and eggs taken from any gall was only six. The following table demonstrates the restricted character of the "nests":—

No. of Gall	Length of Cavity	Diameter	Contents
1.	13 mm.	5 mm.	1 adult, cleaning interior
2.	12	4	1 adult, 1 egg, 5 larvae
3.	18	4	1 adult
4.	18	4	2 larvae, 1 adult
5.	20	5	2 larvae, 1 adult
6.	18	5	1 Acarid mite, 2 larvae
7.	17	4	1 full-grown larva
8. By collector	18	4	3 old and 3 young larvae, 2 eggs
9. By collector	17	3	2 old larvae, 3 eggs

The *Exoneurae* are singularly free from Acarine parasites, but No. 6 gall contained a milky-white mite, which did not do more than clamber aimlessly over the wall of the chamber. Mites are exceedingly numerous in the nests of the earth-digging halictine bees (Rayment, 1935), and have an important function in maintaining the nests in a sanitary condition, but the amount of excretal debris in *Exoneura* nests is very small indeed. The above mite proved to be a European species, *Tyrofagus tenuiclavus*; the first record for Australia.

The collector sends a note stating that he found an entirely black bee in one nest, but dimorphism must be exceedingly rare in the genus, for although the author has examined many hundreds of *Exoneurae* he has not yet observed this phenomenon. It is known that individuals of two or more species will sometimes congregate in a nest for shelter, and perhaps "mutual comfort", but this habit of seeking the company of relations is strongly developed in many genera, but especially in *Paracolletes*, *Halictus*, *Nomia*, *Anthophora*, *Asaropoda*, and, of course, the hive-bee *Apis*, for it is the element of the swarming instinct.

The largest "tube" in any plant stem measured 31 cm. in length in a twig 9 mm. in diameter, the bore having a diameter of 3 mm.; the smallest sticks are only 5 mm. in diameter, so that the external walls are extremely thin.

*Exoneura hamulata* Ckll. is a larger bee, consequently its tube has a diameter of 4 mm.; however, the majority of the species make a bore about 3 mm. and, in a few tubes, there was a blackish skin wad, very thin, at the base, and it may have been formed of discarded larval skins.

#### PLANT-STEMS BORED BY EXONEURAE.

Common Name	Specific Name	Locality	State
Banksia	<i>Banksia serrata</i>	Heathcote	N.S.W.
Bottlebrush	<i>Callistemon</i> sp.	Frankston	Victoria
Blackberry	<i>Rubus</i> sp.	Dandenong	Victoria
Brush Box	<i>Tristania conferta</i>	White Swamp	N.S.W.
Dahlia (Garden)	<i>Dahlia</i> sp.	Dandenong	Victoria
Coral-tree	<i>Erythrina</i> sp.	Lane Cove	N.S.W.
Golden Spray	<i>Viminaria antarctica</i>	Neerim	Victoria
"	" <i>denudata</i>	Cranbourne	Victoria
Grass-tree "	<i>Xanthorrhoea hastilis</i>	Fraser Park	N.S.W.
"	" "	Lane Cove	N.S.W.
"	" <i>minor</i>	Lane Cove	N.S.W.
Hydrangea (Garden)	(Introduced)	Mt. Macedon	Victoria
"	"	Lane Cove	N.S.W.
Lantana "	"	Patonga Beach	N.S.W.
"	"	Lane Cove	N.S.W.
Paper-bark	<i>Melaleuca ericifolia</i>	Frankston	Victoria
Rush Giant	<i>Juncus pallidus</i>	Grampians	Victoria
Rose (Garden)	<i>Rosa</i> sp.	Dandenong	Victoria
Snow Daisy-bush	<i>Olearia lirata</i>	Neerim	Victoria
Spear Grass or			
Saw Sedge	<i>Gahnia tetragonocarpa</i>	Grampians	Victoria
Tree-fern	<i>Dicksonia antarctica</i>	Neerim	Victoria
Wandoo	<i>Eucalyptus redunca</i>	Bolgart	W.A.
Wattle	<i>Acacia</i> sp.	Lane Cove	N.S.W.
Wild Parsnip	<i>Didiscus pilosus</i>	Clyde	Victoria
" "	<i>Spartium junceum</i>	Cranbourne	Victoria
		Lindfield	N.S.W.
Galls (not bored)	<i>Pultenaea stipularis</i>	Sydney	N.S.W.

#### LARVAL DEVELOPMENT.

Critical examination of a large series of plant-tubes shows that in the black species *E. roddiana* and *E. rufitarsis* the eggs are attached to the wall, and project into the lumen at right angles, being fastened at the caudal pole with a clear agglutinative, a secretion of two glands in the apical segments of the female abdomen. The "gum" is exceedingly tough, and attaches the egg very firmly indeed to the wall.

The egg is rather broader in proportion than the average of bees' eggs, but little bowed and milky-white, measuring 1,200 microns at the long axis, and 433 microns at the short, which is a large egg for so small a bee.

An egg of *E. perpensa* Ckll., measured just before hatching, reached the extreme of 2,100 microns at the long axis, and 500 microns at the short. Since the "fresh" egg of this species is about the same size as that of *E. rufitarsis*, they undoubtedly increase in length just before hatching, and by transmitted light, the developing embryo may be seen as an opaque patch in the large mass of the clearer yolk, the deutoplasm. The beautiful hexagonal sculpture, which is so conspicuous on the chorion of the egg of the honey-bee, is not evident on the egg of *Exoneura*. The eggs of the red-bodied *E. concinnula* are attached in a similar manner, but are widely separated, in no particular order, and only two or three are present.

The eggs of *E. rufitarsis* are disposed along a slightly spiral line, and spaced approximately a millimetre apart. They are deposited generally in groups, although there may be only a single egg, or as many as eight. Although more often than not, in such a case, three or four of the eggs have hatched, without altering the original position; six is the commonest number.

In certain of the red-bodied species, such as *E. angophorae* Ckll., the eggs, a dozen or so in number, may be deposited criss-cross in a mass at the base of the chamber, on a communal store of crumbly pollen, and the larvae appear to be able to mount the wall, and attach themselves by the long-pointed "tail". The author had several in an experimental wooden cell, and, during the night, they "climbed" out, thus providing evidence of the larval ability to travel to a new position. Some of the red-bodied group also deposit their eggs in a line.

Several "nests" of *E. rufitarsis* were under constant observation, and at a temperature of 10 deg. C. none of the eggs showed any observable change until the 1st of August, when the merest traces of segmentation were to be seen under a lens. These eggs were probably deposited on the 12th of July, so that 20 days had elapsed. Rodd recorded about 18 days in the warmer climate of Sydney. This is a very long period compared with the three days of the honey-bee in the warmth of the beehive, i.e., 35 deg. C.

Very young larvae showing short "arms", and which were very probably 21 days old on the 12th of July, did not make any evident growth by 1st of August, although they had been constantly attended, nursed and fed with secretion by six females present in the stem. The larvae consumed food throughout September.

The appendages showed signs of being absorbed about 1st October, and had disappeared by 12th October. The pupae were recognisable as such about the 27th October, but at that date they were entirely white, and the compound eyes did not show any colour until 6th November. The bees were finally pigmented and ready to emerge as imagines on 5th December.

The temperature in the field, for the first half of July, 1948, seldom exceeded 12 deg. C., for the the winter was a severe one, and the lower readings established a record. Night temperatures were, of course, much lower.

The egg appears to merge almost imperceptibly into a segmented larva, for only the smallest trace of a twisted white "thread" remains to represent the original chorion of the egg. The strange-looking creatures project like tiny crosses from the wall; the "cross-arms", of course, being the short appendages which soon appear. As the larvae grow they ascend the walls, and dispose themselves at regular intervals according to their age; the oldest always being at the higher end of the chamber, nearer the entrance. It was seen that the adults frequently "brush by" the larvae, even pressing them temporarily "flat" against the wall, but they swing back into their original position immediately the mother passes.

The eggs are deposited by the several sisters inhabiting the tube, and large numbers of eggs have been counted in one tube when eight or so females were present. (See under heading—"Behaviour of the Individual.") Usually it is found that where three females are present there will be eighteen or so eggs. (Compare the limited number of eggs in *E. concinnula* Ckll.)

On the 12th July, 1948, a twig of *Viminaria*, from Clyde, contained the following bees in a cavity 20 cm. deep, seven females, ten males, twelve larvae, but no eggs.

In a fern-frond bored by *E. hamulata* Ckll twenty-six larvae and eleven eggs were taken from two "nests", together with nine females; no males were in the series, but that is not the usual condition, for several males are more often than not present in the chamber.

The larval appendages provide the best specific characters. Some species, such as *E. rufitarsis* and *E. roddiana*, have only one "arm", terminating in a slender "finger", and are very distinctive.

*Exoneura angulata* Raym. is a distinctive species with much black hair on the hind legs like *E. angophorae*, but that bee has black on the abdomen. However, it is easily known from all others by the angulated "face". It was bred from dry stems of the garden *Hydrangea*, and several females were present to attend to the numerous larvae which were lying together in a squirming mass



at the base of the chamber. Each of the larvae had its own individual pudding of pollen. There were 17 larvae and six eggs in one "nest" with several female adults.

On cutting a sliver from the stem to expose portion of the interior, a female immediately ran forward, and carried a larva back to shelter. She repeated this manoeuvre several times until all the larvae had been taken under cover. (See Chadwick's observation under "Behaviour".) This species apparently feeds pollen very early.

The fully developed larvae resemble those of *E. richardsoni* Raym. in having a large number of abdominal nodes, although they are shorter, and it would appear that *angulata* and *albolineata* are allied. The thoracic appendages are different, and a description of the larva is appended.

The fresh egg is typical, but a trifle longer, 1,500 microns at the long axis and 500 microns at the short.

The larvae are of a bright pale-orange colour, and when curled tightly measure 3 mm. in diameter; when fully fed and straight, nearly 6 mm. in length. They have a strong instinct to cluster together and squirm about each other. There are eleven appendages on each side. The first is the longest, one "arm" with one exceedingly long "finger", and two short "fingers", then six short abdominal nodes, next one longer, then two very long, and a shorter one. There is an inner row of microscopic tubercles.

Even the very small larvae were pale-orange, and it was evident that they had consumed some pollen, for it was visible in the mesenteron. Seventeen or so were transferred to bee-hive pollen mixed with "royal jelly" on 3rd November, 1948, but all failed to pupate.

Contrary to the opinion expressed by the author in 1948, he is now convinced that the so-called pseudopodia are actually exudatoria, as Rodd suggested, for he has observed in two species at least, *E. richardsoni* Raym. and *E. angulata* Raym., the larvae apparently sucking the many nodules and appendages.

At times the two "thumbs" of the largest appendages of *E. angulata* are in the mouth together, but most often only one is sucked at a time, and may be held in the mouth for a long period—two minutes or so.

The larvae swallow a few "mouthfuls" of pollen mixture, and then stretch themselves vigorously and quickly backwards three or four times as though endeavouring to "force" the pollen down into the mesenteron. They just as quickly contract several times into a circular bend as though struggling to reach the longer hind processes with the mouth. This exercise is a common and frequent action, and occurs after every few mouthfuls of pollen, and one node after another is touched with the mouth, although not held as is the "thumb" of the large appendage. Even the second row of microscopic nodes is licked and licked again. It was observed that the apex of the nodes is hyaline, and it may be slightly drawn in for a second, when it becomes somewhat flaccid. It suddenly becomes turgid and larger, and the larva touches it with the mouth. Sometimes three or four consecutive nodes are sucked, but it appears to be an effort to reach the apical ones.

The "thumb" is sucked most often, the large appendage is occasionally used as a prop or support, and it was often bent and twisted as the larvae struggled about on the ample communal pudding supplied by the author, but it does not appear to suffer any damage. The larvae ate, with apparent relish, a mixture of "royal jelly" from a queen-cell, and pollen taken from hive-bees, but none survived.

Contents of "nests" of *Exoneura angulata* Raym. in dry stems of *Hydrangea* taken at Essex Park, Dandenong, Victoria, October, 1948:—

No. of Stem	Length cm.	Adult		Eggs	Puddings
		Females	Larvae		
1.	10	4	17	6	7
2.	5	2	4	7	0
3.	7.8	2	0	4	0
4.	11.5	7	14	4	9
5.	17.5	11	0	0	0
6.	17	4	18	6	22

A lone female was sheltering in a small cavity, and two females were in another. Two of the sticks exceeded 7mm. in diameter, and the gallery went down in a spiral, clockwise. No larva was more than 5 cm. from the base of the "nest", and none of the eggs was attached to the walls of the lumen; all were deposited criss-cross among the small larvae and puddings at the base. The puddings were bright-yellow in colour, and the grains oval; only one pudding in five contained triangular grains (*Leptospermum*). The *Hydrangea* was growing in a shaded position.

Early in November, 1948, at Dandenong, the author and his collector, Owen Dawson, found a long series of "nests" of *E. richardsoni* Raym. in dry stems of bramble and rose in the garden at Essex Park, the country home of W. R. Richardson, Esq., to whom the species is dedicated in appreciation of his hospitality and co-operation.

#### IN BLACKBERRY STEMS.

No. of Stem	Length cm.	Adult		Eggs	Puddings
		Females	Larvae		
1.	2.5	1	—	—	—
2.	4	1	—	—	—
3.	13	5	23	6	1
4.	10	4	18	—	—
5.	12.5	4	20	10	—
IN GARDEN ROSE STEMS.					
6.	15	6	16	6	—
7.	11	6	28	10	—
8.	10	1	1	—	—
9.	12.5	6	17	8	8
10.	10	2	3	4	—
11.	15	4	18	3	3
12.	12.5	4	5	—	—
13.	11	6	8	3	—
14.	10	4	—	—	—
15.	10	4	12	7	7
16.	12.5	2	—	—	—
17.	7.5	4	3	6	2
18.	10	2	5	3	2
19.	10	4	—	—	—
20.	10	2	8	4	—
21.	10	8	12	—	—
22.	4	4	12	2	—

This "nest" contained a mixed population, for there were two species, *E. angulata* and two *E. richardsoni*, and both appeared to be feeding the young.

A small black species, *E. rufitarsis* Raym., favoured the dry stems of garden *Dahlia*.

The author has studied many series of "nests" constructed and occupied by *Exoneura asimillima* Raym., and this species may be taken as typical of the group which deposits the eggs first, in a mass at the base of the chamber, and later provides a supply of rather dry mealy pollen in the interstices about the eggs.

All the larvae feed from the common store until they are well developed. After the appendages are absorbed, the larvae rest along the lumen of the tube, heads and tails touching. The supply of pollen is augmented daily, and the mass becomes more compact, with a larger proportion of honey, as the larvae grow. The youngest larvae are, of course, progressively fed with a secretion from the pharyngeal glands of the head.

The first "nests" in the stems of "Saw Sedge", *Gahnia tetragonocarpa*, and "Giant Rush", *Juncus pallidus*, were collected by Owen Dawson at the type locality, Grampians Range, Western Victoria, on 4th December, 1946.

Another long series was taken by this collector on 20th November, 1949, at Cranbourne, Southern Victoria. Twelve dry flower-stalks of "Grasree", *Xanthorrhoea minor*, contained females and larvae in many stages, and the average number of progeny for one mother was six.

The pieces of stems were broken off 13 cm. in length, with a diameter of 8 mm.; the "bore" was 3-4 mm. in diameter and the longest measured 12 cm., the shortest about 3 cm., but these short ones were in course of construction; the average length of the completed bores was 5 cm. Two "nests" contained only very small larvae; one only eggs, no pollen; three females were present in three; two females in two; four of the "nests" contained only one female each. In no case were the larvae distributed along the lumen of the tube.

The original flower-stalks of the Grasrees were about one metre tall, and dry, as they were grown in the previous year. The entrances were made where the pithy interior had been exposed on the end. In a few cases the entrances were through the woody side-wall, but these holes were the work of some other insect. The *Exoneuræ* cannot penetrate hard fibrous structures.

In all the larger stems the entrance is contracted with a neat ring of wood-pulp.

The pollen-grains in these stems were triangular in shape, and had been collected from one plant, very probably *Melaleuca ericifolia*—or perhaps *M. squarosa*—which was abundant in an open gully among the sandhills, which are exploited commercially for the excellent sand. The aspect was N.W.-S.E.

No individual puddings were present in this series of "nests", but the oldest larvae were at the resting stage, and the appendages had been absorbed. Several of the older larvae from the Grampians had individual puddings, but as there is definitely some co-operation with females of other species, these may have been the progeny of an alien mother, or the habit may vary. Because the social habit is developing in the *Exoneuræ*, the mothers of one species will feed secretion to the progeny of other females, and this complicates the investigations, and at times one is not entirely satisfied that all the larvae present in a populous nest are of one species.

Three or four species of females are exceedingly close in morphological structure, and difficult for the student to determine correctly. *E. asimillima* Raym. is very close to *E. holmesi* Raym., which has a light ferruginous-red abdomen and amber tegulae, with considerable long white hair on the "face", whereas *E. asimillima* has a dark blood-red abdomen, and the hair of the head is black. Over a series this is the larger, more robust bee, with black tegulae. All have red legs.

Another very close species is *E. oblitterata* (Ckll.) Raym., but the larvae have only one long "finger" on the larval appendage, whereas *E. holmesi* larvae have three "fingers".

The "fingers" on the appendages of *E. asimillima* are small, and the larvae are clearly in the *E. hamulata* group.

The first appendage has three "fingers"; the second a short basal one; the third is simple. The other segments of the abdomen have short inconspicuous



nodes. The larval appendages are of the greatest value to the taxonomist, and in the absence of the larvae, the adults are often exceedingly difficult to separate.

At Essex Park large numbers of colonies of *E. richardsoni* Raym. were established in the dry twigs of a climbing rose that covered a garden arbour about sixty feet in length; consequently, the majority of the nesting sticks were in more or less permanent shade, for the arbour is ten or more feet in width.

Since the nests were seldom higher than the observer's head, the large aggregation of both bees and sticks could be studied very conveniently. Stems investigated during the first week in December, 1948, were very populous, for they contained males, many females, eggs, puddings and larvae, and the flight of field bees was heaviest at that period, even though most of them were in shade. Mid-summer, then, sees the maximum in activity for this species, and this holds for all of the *Exoneuræ* studied during this investigation.

By autumn the curve on the graph goes down steeply. On 6th March, 1949, numbers of sticks were investigated, and a large percentage contained only a lone female, with three or so eggs which had been deposited loosely at the base of the lumen, and among several pellets of rather dry yellowish pollen. These are the colony-founding females which had departed from the parent nest to find a suitable stick for a new nest. A small percentage of sticks housed a solitary male apparently sheltering.

In *E. richardsoni* the eggs were deposited "criss-cross", without order, at the base of the chamber, among the communal food, but when the growing larvae require individual attention they are disposed up the wall at regular intervals. This habit is in contrast to that of *E. roddiana* Raym., which deposits its eggs in a low spiral line on the wall, and it would be interesting to discover whether or not this latter habit holds goods for all the black species of *Exoneura*.

Up to seventeen pupae in advanced stages, together with a few callows, were present in many nests, and it was evident that these were the last of the second brood for the season. The colony-founding mothers represent the earliest individuals, and these pass through the winter nursing their progeny which form the first brood of the succeeding spring. The activity, then, reaches the minimum during the winter months of May, June, July, but does not cease entirely at any stage.

The larva of *E. lawsoni* Raym. has two "fingers" on the "arm", and there is a basal "thumb", but the adults are black, and approach *E. rufitarsis*. In addition, *lawsoni* has six long processes on the apical ventral segments of the abdomen, *E. hamulata* Ckll., a larger red-bodied species, has eight lateral "arms", with three "fingers" on the first and second pair; one on the third pair, and a short nodule on the fourth pair.

Another species, *E. sub-baculifera* Raym., has a prominent "teat" on the vertex of the head, and Norman Rodd suggested that the adults might obtain a secretion from these protuberances. Wheeler has pointed out that this actually occurs in certain ants. The larvae of *E. baculifera* Ckll. have only a very small cephalic node or "teat", and only rudimentary lateral appendages.

Rodd suggested that the unique teat-like cephalic node on the larvae of *E. sub-baculifera* Raym. may be an exudatorium, such as is present on certain ant larvae, i.e., *Pachysima latifrons*, the adults of which obtain an exudate, a lipoid, from the appendages; ant-larvae are known to exude fatty substances. Rodd suggested that male *Exoneuræ* may obtain such an exudate, hence their continued association with the "nest".

Rodd observed the larvae of *E. roddiana*, each with a ball of pollen held between what Friese terms the pseudopodia, and Wheeler himself prefers this name. The latter author says that the pseudopodia of *Allodape ceratinoides* hold the pollen-ball to the buccal parts. Holmgren thought that the several castes in ants may be due to "exudate hunger", i.e., food castration.

It was observed by the present author that the "arms" on larvae of *E. rufitarsis* Raym. did appear to be larger on some occasions, and he saw a female adult lick one. On another occasion he observed a nursing female feed secretion to an adult male. In any case, the larvae are fed probably for 20 days with the secretion, and after that pollen may be observed in the mesenteron, but never in the tightly-packed manner of *Halictus* and many other genera.

The individual pollen-ball is supplied to the larvae at about 50 or so days after hatching, and the yellowish (greenish on Pollinite) mass is then visible in the mesenteron. This is much slower than what obtains in the bee-hive, where the larvae are fed for about eight days.

It will be seen that while it is extremely difficult to separate the many field bees closely resembling *E. angophorae*, yet the larvae are very different, and it is unwise in many cases to write specific descriptions of new species in the absence of the larval forms. There are so many very critical species.

The appendages reach their full development just about the time that the larvae are fully fed, but as metamorphosis is approached, the appendages are gradually absorbed, and then the taxonomist will be misled by their absence. The largest larvae measured over 3,000 microns in length.

In the "Victorian Naturalist", April, 1946, the author suggested that the "arms" could be used for clinging to the few silken threads on the wall of the tube, but he has now definitely established that the larvae adhere to the wall by the long tapering anal end, which is unique in bees.

The author had a number of "nests" of *E. rufitarsis* under continuous observation, and the females were observed to apply the mouth to the head of the larvae, and it was possible to see the transfer of a clear liquid, probably food. The "champing" and "mouthing" of the larvae indicate that they are requiring food. After the females attend to them the "mouthing" action ceases, and the larvae lapse into a resting-phase. By transmitted light it was possible to observe the processes of digestion in the mesenteron, which contained a pale-yellowish liquid. The contents "boiled" up in rhythmical ebullitions, like a miniature geyser, and then fell back again, and after each eruption the liquid became paler. Minute bubbles appeared to rise from the epithelial cells and mingle with the food. This led the author to postulate that enzymes were being released and incorporated in the mass. The author was able to study under a lens the feeding of a secretion, by the several sisters, to the larvae in a tube. The female bends the slender glossa back under the head, and opening wide her mandibles, takes the tip of the larval head right in between her open jaws, which do not move.

A clear liquid is then exuded on to the larval mouth for a second or two. This is undoubtedly a copious secretion of the pharyngeal glands, and the larva injects it with a conspicuous "mouthing" of the "lips". Another adult female will sometimes "kiss" the larva after its feeding as though it were wiping the soiled mouth of the infant. There is evidence of continued care and gentle attention by all the mothers, but the glossa plays almost no part in the feeding, for the secretion appears to flow from the salivarium. (See "Behaviour of the Individual", below.)

The author has not observed a store of food in any of the many "nests" investigated by him, and to test whether or not the larvae could or would eat a pollen substitute he provided hungry larvae with pollen taken from the cells of the hive, and also a synthetic pollen which he had evolved, and the oldest larvae made a meal from both. Of course no adults were present at this experiment.

The adult bees, too, repaired to another pollen-mass provided by the author, and opening the mandibles to their widest extent, plunged them into the soft batter of honey and pollen; the mandibles do not appear to move, yet the batter could be seen moving into the mouth as though it were being drawn in by suction. The long slender glossa is bent back under the head during the meal, and does not appear to play any part in the action.

It is definitely established that there is no food stored in the communal chamber; that the pharyngeal glands of the females are well developed, and that a secretion is fed to the larvae; a certain amount of pollen is incorporated later; and finally each larva receives its individual ball; and that progressive feeding is the rule of *Exoneura*.

The author had difficulty in bringing the larvae through metamorphosis, probably because the presence of the adult nurses is essential for their proper development; consequently, he determined the time required for the transformation to be approximately 152 days.

It was observed that ever and anon the adults apply the "mouth" to the cephalic pole of the egg, and stroke it downwards two or three times with the fore-legs—it appears to be a cleasing with the tarsal brushes. The action is repeated on the larvae. It is a remarkable fact that only a few of the many spring "nests" studied contained a pupa, although there were numbers of well-developed larvae present. Many pupae are present in mid-summer and autumn.

That the larvae are able to survive long fasts is demonstrated by the following experience of the author. On the 8th June, 1946, he visited a sandstone gully at Lane Cove, Sydney, and collected several "nests" of *E. roddiana* Raym. in *Acacia* twigs, and these were packed in a tight tin container. The author returned to Sandringham, Victoria, after a month of travel on 8th July, 1946, but a chain of circumstances prevented him from examining the "nests" until 90 days later. When the package was opened, the author was astonished to discover that the larvae and adults were still very much alive. All were positively without food for that period. Rodd, too, observed that the bees are capable of surviving long periods of abstention.

There are no distinctive characters on the pupa; no abdominal nodes and spines as in *Halictus*, *Parasphecodes* and *Nomia*, for it has the typical form of the social bees' babies. There are two or three spines on the legs, i.e., strigilis and calcariae.

It was of interest to discover that larvae, feeding on a pollen-ball supplied by the author, showed a blackish mass, at the caudal end, about 24th October, and in a day or two a cylindrical pellet of excreta was voided. The junction of the proctodeum and the mesenteron must occur much earlier than in the hive-bee, and while the larval feeding is drawing to a close.

In the unnatural conditions inseparable from the author's experiments, 152 days were required for the development of the bees from egg to imago, and it might be argued that growth had been hampered by unsuitable food, but an examination of the "nests" on the tea-tree branch on 1st November revealed similar conditions. These could be relied on because the date of the installation of the mothers in the stems was known and, thereafter, they had been left to their own resources. The feeding period of 30 days with secretion and 40 days with pollen is certainly very remarkable if that be the normal time.

#### BEHAVIOUR OF THE INDIVIDUAL.

In winter, from the middle of July, the bees are sluggish, but there were many eggs, and a few young larvae in colonies of *E. roddiana* and *E. concinnula*, and *E. rufitarsis* even at that early date. Surprisingly, the bees do not, like all other wild-bees, dash out to the light when their tubes are opened and attached to the branch, but for safety, it is better to open the sticks at night, leaving the bees to emerge in their own time on the following morning.

Like all other bees, both hive and wild, the actual doorway is examined first with extreme care. The bees walk round and round the periphery, evidently memorising the details, not venturing far on the initial excursions, and returning by the same path.

The earliest appearance of females of *E. richardsoni* from the experimental tubes was on 1st September, 1949; August was distinguished by many warm



days, with a subnormal precipitation. When September opened, the temperatures registered max. 22.6 deg. C., min. 5.5 deg. C., and at 11.30 a.m. two energetic females emerged from one stem for a short flight of less than a metre. They were followed soon after by three females from other stems, but all returned after re-orienting the sites of the nests; three others departed to harvest in the field. A male was observed to issue from one stem and depart. He did not return until 35 minutes later. The bees seldom flew at lower temperatures.

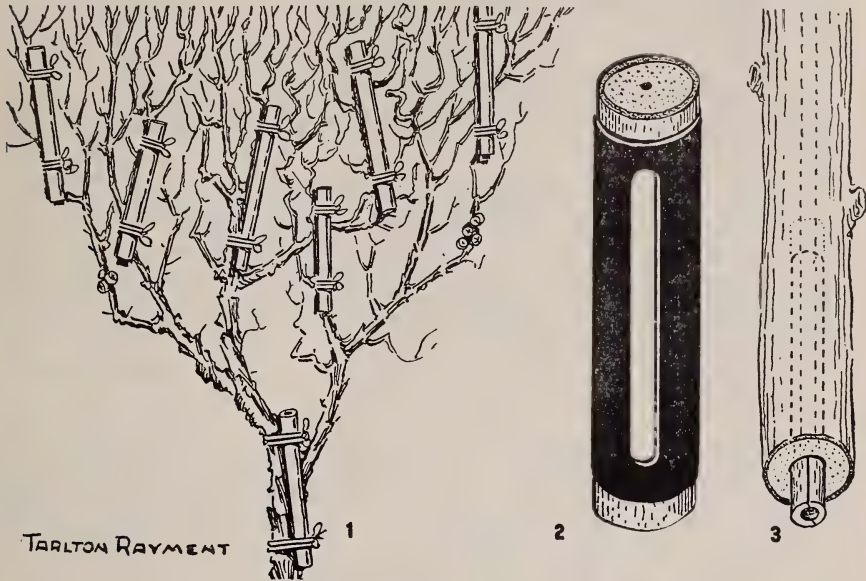


Fig. 2.

1. Dry branch with short lengths of *Hydrangea* stems tied on at convenient levels to attract the reed-bees *Exoneura rufitarsis* Raym.
2. Black sleeve over a stick, with a clear "window" for observation of the larvae.
3. A split stem with a nest is inserted at the base of a larger stem.

They descend into the tube and re-emerge many times to sit in the warmth, preening themselves, exercising their wings and brushing the body. The first flight is merely of 30 or so centimetres, made with the head facing the doorway. Longer and longer flights are made successively, as the "map of the country" is plotted in the insect's brain. These experiments in orientation are repeated so often that the observer's patience is sorely tested. Unlike other wild-bees, the males of which never return to the "nest", and therefore have no need to memorise the way home, the male *Exoneurae* never desert the family; consequently, they are as meticulous as the females in orientating the site of the "nest". (Refer to "Larval Food".) The bees are certainly not nervous, suspicious or aggressive, for the observer may, with a very fine brush, actually guide the sunning bees back into the tube without causing them to take wing. They do not resent the author's close presence, and betray no interest whatever in the movements of the lens.

Should any bees emerge suddenly before they have orientated their new homesite, they will be lost, for then they cannot return. When they appear of their own volition they will re-orient themselves.

The bees do not take wing immediately on emerging, but only after a long survey of the sunny surroundings do they fly on short courses, zig-zagging con-

stantly as they advance and retreat, with the head always directed to the aperture of the gallery. The pattern of the flight is very different from that of *Halictus*, which, having no obstacle in the near vicinity of its individual shaft, performs a number of circular sweeps.

There is no doubt that the close proximity of several galleries amid a tangle of other dried twigs is responsible for the reed-bees' care in orientating the "nest" accurately. The pattern of bees' memorising flights is due to the nature of the environment. Such flights take place only during the warmest hours, between 11 a.m. and 3 p.m.

The cavity of the tube is frequently blocked by the flattened apical tergites of the abdomen. Males have been observed to hover, alight and enter the tube, and immediately block the entrance as described. The action is common to both sexes, and has been observed also in very different earth-digging halictine bees.

In the half-cylinders the bees have no necessity to roll over in a ball when they reverse, but the action must be instinctive, for very frequently they turn in this surprising manner. The "ball" is, of course, formed by tucking in the head and the abdomen until the "body" is of the same diameter as the tube—it is a case of "heels over head", rapidly and very neatly performed. The pithy debris near the door is pushed out by the hind legs and the tip of the abdomen, in the form of very fine shavings, but the boring is a slow process, although the material is both soft and light.

In the tubes, the females of *E. rufitarsis* Raym. frequently dropped a globule of a secretion on the interior walls.

It was early evident that six females in a tube secreted far more food than could be consumed by the nine larvae; consequently, the surplus was exuded on to the wall. The author succeeded in getting a globule or two placed on a glass slip, when it was seen to be microscopically granular, with a slight milky opacity, and giving an acid reaction. Every now and then two females will approach and "kiss" each other—that is, the mandibles do not open, but the maxillary and labial palpi of both bees are extruded and moved about rapidly as they "caress" each other. On several occasions it seemed that some liquid passed from one adult to another. The long glossa was bent back under the head and did not function. The author would say that some secretion is available, for he observed that after a female had fed a larva, another female would come along and sip a trifle from about the mandibles of both the adult and the baby as though "wiping its mouth".

The bees have frequent "rest" periods, when they stand immobilised for a minute or two; then the abdomen will pulsate rapidly for a little longer, during which time it can be seen that the ivory-coloured "thread" of the oesophagus, nerves, etc., at the foramen is also pulsating in rhythm. There is, too, a short phase when the thorax is vibrated vertically very rapidly. The bee then resumes other activities. If one sister unexpectedly encounters another, the mandibles are held wide open, in a threatening gesture, but after a "kiss" both go on their way. The bees are exceedingly "light on their feet", for while they often walk over the eggs and the larvae, yet they never inflict the slightest damage to either.

In the galls observed by Chadwick the adult females carried the larvae from place to place, and this action was observed by the author in several of the "nests" investigated by him; the transportation of the larvae may have been due to panic when the adults were suddenly exposed to light. That observer also saw the females of *E. concinnula* closing the entrance with the subapical segments of the abdomen.

A deal of time is devoted to cleaning the body. The antennae are constantly combed and brushed by the anterior legs, as is the long glossa, and the head and eyes. The median legs are turned up over the thorax, which is

kept highly polished, since there is little hair; the median pair also clean the upper surface of the wings, and assist in the toilet of the hind legs, the wings are pressed flat under the abdomen, and the under surface is then vigorously brushed. The gaster is cleaned by the posterior legs, and the pair are constantly being brushed together. Every now and then the wings are given a sudden flick or two. Considerable time and energy is expended on the toilet.

The introduction of a strange male to five females in a tube under observation produced no evident reactions, the bees showing no interest whatever in the stranger, but it should be remembered that the conditions were unnatural, and scent did not appear to have any significance.

A few excessively tenuous threads are "licked" on the walls of the tube, and the tip of the glossa travels over the surface without haste. Every now and then the head-capsule is rolled rapidly from side to side as the front legs curve round the genae and the compound eyes. The whole action suggests that of a man bringing his bowed arms alternately up over his head quickly. It cannot be a mere matter of cleansing, for the polished head is immaculate. The author suggests that this remarkable action excites the glands of the head. (See fig. 4, pl. xxvii.)

These two organs in the *Hymenoptera* are the cause of some confusion to certain authors, who refer to the secretions of both glands as saliva. Indeed, one says the eggs of certain ants are stuck together with saliva, but probably the mucous glands in the apical segments of the female abdomen are the source of the "egg-glue".

#### ENEMIES AND PARASITES.

Like all other bees, the *Exoneuræ* have several enemies, endoparasites and ectoparasites are present, and of the former, minute chalcid wasps in the Family Encyrtidae are the more numerous.

Norman Rodd, Lane Cove, sent to the author the dry shell of a red reed-bee, probably *Exoneura angophoræ* Ckll., which contained a large number of hymenopterous larvae disposed in close symmetrical rows. The body of the host had been reduced to the merest dry skin, for the whole of the interior had been consumed by the horde of parasites. These were reared to maturity, and the adult wasps proved to be a new species, for which the author proposed the name *Aphycus asperithorax* Rayment, 1949. The tiny wasps could easily enter the plant-stems in which the reed-bees "nest" and insert an egg in every larva, for there are no protective obstacles, such as woody cell-divisions, in the communal chambers, and although the aperture of the bee's tube is small, sometimes less than 3 mm., yet these parasites are much smaller.

However, the chalcid parasites are also successful even when there are several cell-divisions in the plant-stem, for the author received such a one from Owen Dawson, Clyde, Victoria. This collector had broken off a dry stem from a plant of *Viminaria denudata*, thinking that it contained a nest of *Exoneura rufitarsis* Raym., but on splitting it, discovered several cell-divisions, with a larva occupying each chamber. Careful investigation showed that a tiny entrance had been drilled through the wall, a condition never present in *Exoneura* "nests". This one proved to be the work of *Hylaeus nigrojugata* Raym., and it was quite typical, for it contained several cells of impalpable silvery tissue, each divided by a hard wad of dark red pollen residue and stercoral debris. It was evident that in no case had the plugs been perforated, and the parasitic female wasp must have entered each chamber successively as it was completed, for all the cells were constructed contiguously along the tube. This stem was collected on 13th July, 1946; that is, in winter, and it was observed that, at that early date, each bee-larva was infested with numbers of still more minute larvae. Metamorphic changes became evident on the 20th September, and most had reached the pupa stage by the 21st September. They were completely black by October 15th, and emerged as imagines about 24th October. An average of 22 was



obtained from each small bee-larva, but they were not disposed in such exceedingly orderly rows as those of *Aphycus*.

The progeny of the reed-bees is not more vulnerable to attack because of the utter absence of such barriers as cell-divisions, for "nests" containing several of these obstacles suffer equally heavy infestation.

The excessive numbers of parasites present in each bee-larva would, at first glance, connote a similarly large deposition of wasp eggs, but the minute size of the wasp—a millimetre—presents certain difficulties for this concept, since the ovaries are not excessively prolific.

It appears that only one egg is deposited by the parasite in each bee-larva, but the egg is capable of a remarkable division, so that dozens of young parasites result from the one ovum—"polyembryony". This phenomenon is not limited to the Encyrtidae, for it occurs in the higher animals, and even in man himself, as when a woman bears identical twins from one ovum.

The author has recovered a partly-digested Acarid mite from the pollen residues in a larva of *Exoneura*, and also what appeared to be a triungulin. It would appear that if a triungulin of *Stylops* enter by the alimentary canal, and reach the mesenteron, then it might leave that organ prior to or at its junction with the proctodeum, and the parasite's ultimate position, between the third and fourth tergites of the imago, is reasonably explained. However, this is a mere speculation.<sup>2</sup>

The bees are remarkably free from Acarine mites,<sup>3</sup> but one was present in a "nest" in a gall collected in Sydney. The reason for this freedom from mites is obscure, for *Lestis*,<sup>4</sup> a large carpenter-bee, living in almost parallel conditions, sometimes has several score of mites on the body. Spiders constructing their webs on shrubs occupied by the bees secure an odd victim, but the captures by this enemy are few, and have little incidence on the success of the species. The small size of the bees, and their rapid flight, apparently bestowed a certain immunity from attacks by birds and entomophagous insects, for in the colonies established by the author at his home only a rare reed-bee fails to return to the "nest" during the working season.

Ants range over most plants, and most often encounter the galleries of the *Exoneurae*, but as there are usually several female bees present in each "nest", ants secure few victims. The size of the aperture seldom exceeds 3 mm. in diameter, and often is less, so that only the smaller black ants can effect an easy entrance. *Iridomyrmex rufoniger* often investigates, but is rarely successful.

#### NOTES ON ANATOMY AND PHYSIOLOGY.

The glossa is exceedingly long for such small insects, and, as in all bees, covered with a mass of setae disposed in a characteristic pattern. In *Apis*, the hive-bee, and in *Exoneura* the setae are acute, but in *Asaropoda* they are spatulate; in *Paracolletes* they are still broader, in *Anthophora* they are leaf-like, and doubtless serve as spreaders of the saliva forming the colloidal membrane. It will be remembered that all animals lick with the dorsal surface of the tongue, and when bees turn the tip of the glossa under and backwards, the setae are then in the proper position for spreading.

2. In the few cases investigated by the author, the abdominal organs of bees parasitised by a stylops did not appear to have suffered any structural damage, and the observer is therefore tempted to formulate a theory. An exceedingly large percentage of bees, *Euryglossomorpha nigra* Sm., from Mt. Canoblas, New South Wales, was parasitised by a stylops, and on one bee the third and fourth tergites had become permanently deformed, but the stylops had disappeared.

3. This Tyroglyphid mite was mounted and submitted to Mr. H. Womersley, South Australian Museum, and he kindly determined it as *Tyrofagus tenuiclavus* Zachvatkin, 1941. It is closely allied to the flour and cheese mites of Europe, and this is a new record for Australia.

4. Deutonymphs of *Sennertis bifilis* Canest., and in the wandering stage they are often present on carpenter bees. I am indebted to Mr. Womersley for both determinations.

There are four segments in the labial palpus, the basal pair being exceedingly long; the maxillary palpus has five segments, although in the generic diagnosis in "a Cluster of Bees" six segments are given in error. The salivarium, near the base of the paraglossae, plays an important function in the physiology of the reed-bees, and the author observed that the secretion of the pharyngeal glands seldom flows down the pseudo-tube of the glossa, but wells up out of the salivarium. When the female is subjected to an anaesthetic, such as ether, a globule will sometimes appear at the salivarium, but generally it will be absorbed before it has time to flow down the glossa. This can be observed quite clearly when the whole of the mouthparts are extruded.

McIndoo (1916) says: "It is strange that both liquids can travel in opposite directions along the same route by no force other than capillarity". He believed that both honey and saliva flowed side by side in the glossal tube. Snodgrass (1925) says this explanation is "too strange, and Nature did not devise the plan". The latter author says he "has no evidence that food liquids ever go up the ventral channel of the glossa". My experiments demonstrated conclusively that in *Exoneura* at least the glandular "pap" does not pass along the glossal tube during the feeding of the larvae, for that organ is folded back clear under the head and, in that position, can have no function as a channel. The secretion of the post-cerebral salivary glands, however, appears to flow along the glossal tube, but this is difficult to observe; only the tip of the glossa is used for draping the wall. The latter author observed a secretion welling out as a clear liquid which swells the glossal channel in honey-bees under an anaesthetic. Snodgrass says this occurs after the insects have been fed on cane sugar for some time. The globule on the salivarium may be seen in wild bees which have never known sugar; indeed, it is present in individuals which have never eaten. In *Exoneura* it is definitely the salivarium which is applied to the mouth of the larva.

The pharyngeal glands of the head are well developed, and resemble a grape-like cluster of pearls when the nursing bees are secreting copiously.

The general design of the alimentary canal approximates that of the honey-bee; a narrow tube passes as the oesophagus through the head and thorax, enlarging into a clear thin pear-shaped honey-sac, again constructed and closed by the minute proventricular valve, greatly expanded as the cylindrical corrugated ventriculus, or true stomach, constricted yet again as the small intestine, and again greatly distended as the rectum or large bowel, and finally constricted to form the anus at the apical segment of the abdomen.

As in the honey-bee, *Apis*, the epithelium of the rectum in *E. rufitarsis* is a thin cellular layer against the cuticular intima of the outer surface. On the anterior half are six rectal glands, circular in form, and clear, resembling ocelli. They are paler and appear to be semispherical, and covered with a microscopic, close network of tracheal tubes.

Snodgrass says that each of the glands in the honey-bees is a "hollow cylindrical tube, with a thick inner wall and a thinner outer wall. When the rectum is distended the glands bulge on the outer surface as six opaque ridges, but when empty the glands sink into the walls and protrude into the lumen". The glands of *Exoneura* appear to have a similar structure.

The rectum of the *Exoneura* examined, males and females, contained a few shells of pollen, but was not unduly distended, although it was winter. The author is unable to say what would be the appearance of the glands if the rectum were excessively distended as sometimes occurs when honey-bees are confined to the hive for long periods by stormy weather.

Trappmann (1923) thought that a secretion from the glands is discharged into the rectum, and Pavlovsky and Zarin (1922) suggested that the glands are a source of catalase, and also bring about oxidising processes. However, the real function of the glands has not yet been satisfactorily explained, but as they are excessively large in the pollen-eating Halictine bees, and small in the species feeding

the secretion to the young, it would appear that Pavlosky and Zarin's explanation is probably correct.

The proventricular valve in *Exoneura* is similar in form to that of *Apis*, the hive-bee. It is quadrangular rather than spherical, and apparently functions in the same manner, i.e., regulating the supply of nectar passing through from the pear-shaped thin membranous honey-sac to the corrugated ventriculus, or true stomach, where it becomes available for the sustenance of the bee, the sac being merely a vessel for carrying the sweet.

In certain hive-bees received by the author from Inverell, New South Wales, and which were dying on the ground under white-box trees (*Eucalyptus albens*), it was found that the proventricular valve was much enlarged, and so congested with pollen-grains that it could no longer function, and the bees succumbed. An exceedingly large yeast was present in numbers in the rectum, but whether or not this had any incidence on the mortality could not be investigated.

There are a few malpighian tubules, about twelve, whereas the honey-bee has perhaps a hundred of them. The tubules undoubtedly function as kidneys, throwing off urates, phosphates and calcium carbonate, and a milky drop or two of these is voided on or before the first flight. It is significant that in the very different genus, *Halictus*, the tubules of the newly-emerged imagines are very yellow with waste products, but these bees are confined to a diet mainly of pollen. The tubules of *Exoneura* are much paler.

The fat body is conspicuous in the imagines, but oenocytes are not prominent in the older larvae, although they are numerous in other genera feeding mainly on a honey and pollen diet, with a minimum of glandular secretion.

The sting of the female is well developed, but incapable of penetrating human epidermis, for the bees are very small.

The genitalia of the males is distinctive, with two fringes of stout spines, and are thus quite unlike the genitalia of other bees.

The author was more than surprised to find that the anterior legs of *Exoneura rufitarsis* Raym. (5 mm. in length) were identical in size and proportion with those of *Halictus erythrus dimorphus* Raym. (5 mm. in length), although the latter is in a very different family of earth-digging bees and, therefore, far lower on the evolutionary ladder than the reed-bees. Such a close likeness is more than co-incidental; it demonstrates the common inheritance of the bees.

#### SUMMARY.

The reed-bees are widely distributed along the eastern and southern littoral of Australia; from Queensland to Western Australia. All the species are small, 3-6 mm. and even less, in length, and none makes any attack on the observer, for they are neither excitable nor aggressive, but docile and attractive.

The "nests" are almost invariably in stems or reeds with a soft pithy core, and there are no cell-divisions, only one communal chamber. The bees have very little constructive ability.

Certain species attach the eggs in a row to the wall; others deposit them criss-cross, loose, at the base of the lumen; some species develop the larvae on a communal pudding. The incubation of the egg takes up to 20 days, and complete development of the larva over four months.

The larvae have unique "arms" and "fingers", and for 30 days or so are fed by the several nurses with a copious secretion of the pharyngeal glands of the head. Later, each larva receives its own individual pudding of pollen, which is held to the buccal parts on the ventral surface.

The imagines and larvae are capable of surviving lengthy periods of abstention from food—more than 90 days, but the experiment was not pressed to the extreme limit.



The larval appendages provide the most reliable specific characters, and, in the absence of the larvae, it is unwise to describe any bee as new, for many species are very critical.

That the pseudopodia function as exudatoria was determined conclusively. The appendages are absorbed on the approach of metamorphosis, and the faeces are ejected while the larva is still feeding, demonstrating that the junction of the proctodeum and mesenteron is effected at an earlier stage than in other bees.

There are no castes, but several sisters remain together in one stem, and attend to all the duties; males, too, are usually present, therefore, the genus must be regarded as a social one, although of a primitive kind.

The experiments with *E. rufitarsis* and *E. richardsoni* demonstrated that not more than two broods, a spring and an autumn one of males and females, are reared each season. The adults have a long life compared with the simple wild-bees, for they live for more than twelve months, and are present in the home when the young are finally developed as imagines. There is, therefore, some support for Prof. W. M. Wheeler's postulation that longevity of the parents is a factor in the evolution of the social state.

The three types of larval development in *Exoneura* have parallels in the South African genus *Allodape*.

There is some exchange of glandular food from one adult to another (Honey-bee workers normally pass honey from one to another, and secretion to the queen).

The rectal glands are larger on genera feeding on a more primitive pudding of pollen and honey with a modicum of secretion.

The bees visit many botanical species in entirely different families.

The dates given in the calendar below are, of course, approximate only, for although several hundreds of larvae were kept under close observation, it was impossible to discern the actual beginning of the change from one phase to another. Moreover, the larvae were subjected to various experiments, and often it was not possible to determine conclusively the incidence of these on the ultimate development of the insect. The mother bees cannot be held indefinitely in the observatory tubes, and the absence of the females for long periods, in the artificial conditions of the laboratory, doubtless militate against the normal development of the larvae. Males are the first to succumb to imprisonment.

#### CALENDAR OF DEVELOPMENT.

##### Female *Exoneura richardsoni* Raym.

Incubation 18-20 days.	7 July, 1948:	A series of females with eggs in plant stem.
	15   "   "	A granular opacity appears in middle of egg.
	20   "   "	Opaque area enlarged, but poles translucent.
	26   "   "	Segmentation visible; eggs hatched, secretion being fed.
Copious secretion 14-20 days.	27   "   "	Females feeding larvae copiously with secretion.
	30   "   "	Progressive feeding with secretion continued.
	5 Aug.	Nodes developing on larvae.
	10   "   "	Copious feeding maintained; nodes larger.
	15   "   "	Nodes developed into defined "arms".
Pollen added 10 days	16   "   "	Mothers adding some pollen to secretion.
	20   "   "	Orange-coloured pollen visible in mesenteron.
	25   "   "	Pollen percentage increasing in food, but secretion decreasing.

Larvae eating pollen-ball 37 days.	26	"	"	Pollen-ball given to larva on ventral surface.
	30	"	"	Larvae consuming pollen taken from hive-bees.
	5	Sept.	"	Larvae consuming synthetic pollen; greenish colour in mesenteron.
	10	"	"	Larvae receive "Royal Pap" mixed with pollen from hive-bees.
	15	"	"	Mesenteron appears to contain much pollen.
	20	"	"	Pellet of excreta aggregating at caudal pole of larva.
	25	"	"	Larvae still feeding. First pellet excreted.
	1	Oct.	"	Desultory feeding by larvae. Second pellet excreted.
Resting phase 30 days.	5	"	"	Feeding ceases; third pellet excreted; larvae writhe on exposure.
	10	"	"	Larvae apparently resting; "arms" almost absorbed.
	20	"	"	Resting phase continues, no movement.
	31	"	"	Pellicle somewhat flaccid, pupa revealed.
Pupal phase 35 days.	1	Nov.	"	Pellicle still attached at caudal pole.
	10	"	"	All eyes faintly pink.
	20	"	"	Eyes dark-pink, lead-colour on head and thorax.
	30	"	"	Eyes, head and thorax all deepest royal-blue colour.
	2	Dec.	"	Eyes, head, thorax deepest blue-black; abdomen pale-amber; all appendages still white; wings dark-grey.
	4	"	"	Only tibiae, tarsi and mouthparts white; coxae, trochanters, femora and antennae blue-black; base of abdomen with dark cloud.
Total period 152 days approx.	5	"	"	Imagines fully developed, but wings milky white; walking with vigour; adult colouring now complete.

The maximum for activity is reached in mid-summer, and during the second week in January the colonies are very populous, with many males present in the stems, and it appears that copulation occurs there; eggs, puddings, larvae, pupae, imagines, are all present at that period.

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#### EXPLANATION OF PLATE xxvii.

1. Adult female, *Exoneura rufitarsis* Raym., "grooming" and feeding a young larva with the secretion; note the glossa folded back under the head.
2. Two adult females during the "kissing" action.
3. One female "wiping the mouth" of a nurse-bee after she had fed a larva.
4. During the "draping" of the walls, the eyes and genae are stroked rapidly with the forelegs alternately as the head rolls from side to side.
5. Adult females turn "heels over head" as they reverse in the lumen of the stem.
6. Portion of the alimentary canal, showing rectum and circular rectal glands (marked by the arrow), malpighian tubules, and portion of ventriculus.
7. Rectal gland more highly magnified to show the close network of trachea.
8. Mandible of female *Exoneurae* is bidentate.
9. Mandible of the male is simple.
10. Genitalia of male *E. perpensa* Ckll.
11. Genitalia of male *E. rufitarsis* Raym. at the same magnification. Note the unique spines.
12. Anterior wing; note the absence of the second recurrent nervure; this character is responsible for the generic name.
13. Anterior wing with five hamuli.
14. Seventh tergite of the male.
15. Myrtaceous pollen-grains removed from the ventriculus of a male.
16. Labrum of the female.

## EXPLANATION OF PLATE xxviii.

1. Egg of *Exoneura rufitarsis* Raym.; note the hyaline caudal pole.
2. Young larva before the lateral appendages appear.
3. Larva soon after the appearance of the appendages.
4. The appendages are fully developed at forty days.
5. As metamorphosis approaches the appendages are gradually absorbed.
6. At one phase the appendages become distended.
7. The pupa presents no distinctive characters apart from the long spines of the tibiae. (All the preceding figs. at same magnification.)
8. Oblique ventral view showing the last phase of the invagination of the apical segments of the abdomen.
9. Larva of *E. sub-baculifera* Raym.; note the prominent cephalic protuberance and numerous abdominal processes.
10. Oblique ventral view of apical processes of *E. richardsoni* Raym.
11. A. B. C. D. First, second, third, fourth lateral appendages of *Exoneura hamulata* Ckll.
12. The pharyngeal glands are well developed in the *Exoneurae*.

## EXPLANATION OF PLATE xxix.

1. Front of head-capsule of female *Exoneura rufitarsis* Raym.
2. Front of head-capsule of male; note the excavated areas about the bases of the scapes.
3. Mouthparts showing the slender glossa and maxillary and labial palpi. The position of the salivarium is marked by an arrow in this and the next figure. Pressure from the cover-glass causes deformity of the parts.
4. Head-capsule of female pupa showing the development of the mouthparts.
5. Portion of glossa highly magnified to show the arrangement of the acute setae.
6. Margin of galea highly magnified.
7. Anterior leg of male.
8. Hooklet of the fifth tarsus of the male.
9. Flagellum of the female.
10. Strigilis of the male.
11. Portion of the opposing comb of the antenna-cleaner.
12. Hind calcar of male.
13. Median leg of male.
14. Posterior leg of female.
15. Two of the forked hairs from the leg.
16. Oblique ventral view showing the invagination of the apical segments of the abdomen.
17. Pharyngeal plate of the female.
18. Ducts of the pharyngeal glands more highly magnified.
19. The delicate sculpturing of the mesothorax.

## EXPLANATION OF PLATE xxx.

Clypeal Markings on Species of *Exoneura*.

- 1- 2. Male and female *E. oblitterata* Ckll.
- 3- 4. *E. lawsoni* Raym.
- 5- 6. *E. rufitarsis* Raym.
- 7- 8. *E. richardsoni* Raym.
- 9-10. *E. asimillima* Raym.; lower portion is suffused in female.
- 11-12. *E. holmesi* Raym.; lower portion is suffused in male.
- 13-14. *E. hamulata* Ckll.
- 15-16. *E. montana* Raym.
- 17-18. *E. abstrusa* Ckll.
19. Male *E. zieglerei* Raym.
20. Female *E. angophorella* Raym; median portion is suffused.
- 21-22. Male and female *E. perpensa* Ckll.
23. Female *E. asimillima* Raym.
24. Female *E. albolineata* Ckll.